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RESEARCH ARTICLE

Potential impact of mammal defaunation on the early regeneration of a large-seeded palm in the Brazilian Atlantic Forest

Impacto potencial da defaunação de mamíferos na regeneração inicial de uma palmeira de semente grande na Mata Atlântica do Brasil

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Abstract

Defaunation, the decline in animal species and populations, is biased towards large-bodied animals that have unique roles as dispersers of large seeds. However, it is speculated that these roles may still be performed by smaller animals, such as small mammals like rodents and marsupials, that thrive in defaunated sites. We investigated if small mammals can disperse the large-seeded palm *Attalea dubia*. We performed the study in a well-conserved Atlantic Forest remnant in southeast Brazil that still harbours large mammals, such as tapirs. Focal observations showed that capuchin-monkeys consumed the mesocarp of the fruits and dropped the seeds beneath the plant crown thereafter. Mammals preyed on ca. 1% and removed ca. 15% of the fallen fruit/seed and deposited them up to 15 m away. Amongst them, small mammals (< 1 kg), such as the squirrel *Guerlinguetus brasiliensis* and non-identified nocturnal Sigmodontinae, as well as the marsupial *Philander frenatus* performed the bulk of interactions. Dispersal enhances recruitment, but the short distances of seed removal did not match the current spatial distribution of palm seedlings and juveniles. Recaching rates of hoarded seeds were small (2%)

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and unlikely to increase distances of seed dispersal achieved. Short distances of dispersal would increase plant clumpiness and negative density-dependent effects with time. Although small mammals can provide legitimate dispersal, they cannot fully replace larger frugivorous mammals and maintain long-distance seed dispersal that feeds plant metapopulation dynamics and seed gene flow.

Resumo

Defaunação, o declínio de populações e espécies de animais, é enviesada para animais de grande tamanho corporal que têm papéis únicos como dispersores de sementes grandes. Contudo, especula-se se esses papéis podem ainda ser desempenhados por animais menores, como pequenos mamíferos como roedores e marsupiais, que prosperam em sítios defaunados. Assim, investigamos se pequenos mamíferos podem dispersar efetivamente a palmeira de sementes grande *Attalea dubia*. Executamos este estudo em uma floresta atlântica bem conservada no sudeste do Brasil que ainda tem grandes mamíferos, tais como as antas. Observações focais mostraram que macacos-prego consumiram o mesocarpo dos frutos e derrubaram as sementes da palmeira sob a copa. Mamíferos predaram ca. 1% e removeram ca. 15% desses frutos/sementes caídos e os depositaram a uma distância de até 15 m. Entre eles, pequenos mamíferos (< 1 kg), tais como esquilos *Guerlinguetus brasiliensis* e Sigmodontinae noturnos não identificados, bem como o marsupial *Philander frenatus*, executaram a maioria das interações. A dispersão incrementou o recrutamento, mas as distâncias curtas de dispersão de sementes não se ajustaram à distribuição espacial atual das plântulas e juvenis da palmeira. Taxas de redistribuição de sementes estocadas foram pequenas (2%) e provavelmente incapazes de aumentar as distâncias de dispersão alcançadas. Pequenas distâncias de dispersão incrementariam o agrupamento de plantas e efeitos de dependência de densidade negativos com o tempo. Embora pequenos mamíferos possam proporcionar dispersão legítima eles não podem substituir completamente mamíferos frugívoros maiores e manter dispersão de sementes em longa distância necessária à dinâmica de metapopulações e ao fluxo gênico por sementes.

Keywords

Attalea; defaunation; seed dispersal; seed hoarding; seedling distribution

Palavras-chave

Attalea; defaunação; dispersão de sementes; distribuição de plântulas; estoque de sementes

Introduction

Defaunation, i.e. the extirpation of animals by hunting, habitat loss, habitat fragmentation, climate change and pollution, may impact several ecosystem processes (Dirzo et al. 2014; Young et al. 2016). Selective defaunation of large-bodied animals produces a downsizing of mutualistic seed dispersal partners with potential ecological, genetic and evolutionary consequences for plant populations (Galetti et al. 2013; Pérez-Méndez et al. 2016; Young et al. 2016). Seed dispersal in tropical forests is likely to be greatly affected, as most trees rely on vertebrates frugivores for seed dispersal and plant regeneration. This is specially true for plants producing large seeds (LSP), as those seeds may only be dispersed in the guts of large-bodied frugivorous animals that match the gape width and mouth sizes necessary to swallow such large seeds (Silva and Tabarelli 2000; Corlett 2007; Peres and Palacios 2007; Ripple

et al. 2015; Neuschulz et al. 2016). Large-bodied frugivores are usually the agents of dispersal to large amounts of seeds to long distances (Fragoso et al. 2003; Giombini et al. 2016), playing a role in metapopulation dynamics (Jordano et al. 2007). Forests which are deprived of these large animals frequently have lots of undispersed seeds of LSP accumulated around adult plants, where recruitment is unlikely to happen due to negative distance- and density-dependent mortality (Forget and Jansen 2007; Neuschulz et al. 2016; Terborgh et al. 2008; Caughlin et al. 2015).

There is a positive correlation between body size and risk of extinction in mammals, with a predictable size-selective defaunation gradient with increasing disturbance (Fritz et al. 2009; Dirzo et al. 2014; Young et al. 2016). While large mammals such as tapirs vanish, some species of small rodents that prey on or disperse seeds remain, even in the most disturbed tracts of fragmented forests (Brewer and Rejmánek 1999; Barnett et al. 2000; Dirzo et al. 2007; Peres and Palacios 2007; Cao et al. 2011; Galetti et al. 2015). Small rodents often prey on seeds *in situ* or scatter-hoard them for later consumption, but some seeds are often not recovered and may germinate. Thus small rodents often have a dual role as seed predators and dispersers (Brewer and Rejmánek 1999; Bordignon and Monteiro-Filho 2000; Carvajal and Adler 2008; Iob and Vieira 2008). Usually, rodents remove seeds to local scales (tens of metres; Choo et al. 2012) and scatterhoard seeds in small clumps, thereby decreasing negative density-dependent effects (Fragoso 1997). Therefore, small rodents may act as surrogate dispersers of LSP in the absence of large-bodied frugivores. However, few studies advance beyond seed stage and attempt to link seed dispersal distances by small rodents to seedling and adult distribution (Forget 1990), thus constraining a proper evaluation of the role of small rodents in plant regeneration.

The aparent short distances of seed dispersal provided by rodents may be enough for the recruitment of LSP far away from parental plants. For instance, hoarded seeds may be recached several times by different individual agoutis that steal seeds from one another (Jansen et al. 2012). As a result, a seed may be deposited hundreds of metres away, mimicking the distances of seed dispersal once provided by extinct megafauna (Jansen et al. 2012). Thus, rodents would be surrogate dispersers of LSP enabling plant regeneration in the long term. However, the evidence of common repeated recaching of hoarded seeds comes from a single site – Barro Colorado Island in Panama – which has an extremely high density of agoutis, well known for their hoarding behaviour (Wright et al. 1999; Wright and Duber 2001). The high densities of agoutis and other small- to medium-sized mammals in Barro Colorado Island are probably the result of predator release, due to the long term absence of top predators such as jaguars, plus protection from poaching (Wright et al. 1999). We do not know if, in sites with more natural densities of small/medium sized rodents, the frequency of seed recaching and the distances where seeds are deposited would be enough to reproduce the spatial pattern of LSP regeneration. As land conversion, poaching and climate change proceeds, large tracts of tropical forests are likely to retain small rodents as the exclusive intact functional group of mammalian seed predators and dispersers (Barnett et al. 2000; Peres and Palacios 2007; Cao et

al. 2011; Galetti et al. 2015). Therefore, understanding the role of small mammals in plant recruitment is crucial to improve our predictions about the effects of defaunation and tropical forest disturbances.

In this study, we investigated the role of small mammals in seed dispersal, seedling and juvenile regeneration of the large-seeded palm *Attalea dubia* (Mart.) Bur. (Arecaceae) in a large and well-conserved site of the Brazilian Atlantic Forest. Our aims were: 1) identify seed dispersers and seed predators; 2) evaluate the fate (e.g. dispersal or predation) of fallen fruits/seeds and the importance of dispersal for plant regeneration; and 3) describe the spatial pattern of seedling and juvenile regeneration and test if small mammal seed dispersal may account for it.

Material and methods

This study was carried out in Carlos Botelho State Park (CBSP), a 37,644 ha protected area covered by old growth humid Atlantic Forest in Southeast Brazil (24°06'55"S, 47°47'18"W). Mean annual temperatures vary between 17° and 22 °C. There is no dry season and mean annual rainfall is between 1700 and 2400 mm. CBSP is neighbour of other protected areas that together cover more than 1 million ha, the largest continuous remnant of Atlantic Forests (Ribeiro et al. 2009). Local non-volant mammalian assemblage reaches 53 species including top predators such as Jaguars *Panthera onca* (Linnaeus, 1758) and large ungulates such as tapirs *Tapirus terrestris* (Linnaeus, 1758), as well as at least 16 species of rodents (Brocardo et al. 2012), several of them potential consumers of fruits/seeds of *Attalea dubia*. This arboreal palm reproduces only by seed and it is endemic from coastal humid Atlantic Forests of Brazil (Lorenzi 1996). In CBSP, *Attalea* flowers between February and April, unripe fruits are presented throughout the year while ripe fruits are more abundant in September-October (A.Y.Y. Meiga unpubl. data). The orange-brown fruits of *Attalea dubia* have a fibrous mesocarp and rigid endocarp known as pyrenium. Throughout the study, we will use generically the term "fruit" to refer to the pyrenium with pulp and "seed" to refer to the pyrenium without pulp. Seeds usually contains only one embryo and are 4.2 ± 0.4 cm in length and 2.4 ± 0.2 cm in diameter (mean ± SD, n = 484), with 16 ± 4 g of fresh mass (n = 12) (Meiga and Christianini 2015).

To record the animals that interact with fallen fruits or seeds beneath the crown of *A. dubia*, an automatic camera-trap (Tigrinus S/A with passive motion and triggered by heat detection) was set under each of five fruiting palms over 24-hours a day for 15 consecutive days (total of 1,800 hours of camera-trap observations) from November 2010 to March 2011. Furthermore, we performed visual observations from October 2010 to March 2011 on other 10 fruiting plants located at least 100 m away from each other. One of us (AYYM) stayed hidden away from a focal plant between 8:00–10:00 a.m. and 4:00–6:00 p.m. during five days (20 h of observations per plant; total sampling effort of 200 h). We recorded animal species that visited the crown or the forest floor around the focal palm and interacted with fruits/seeds, as well as the number of fruits/seeds with which the animal interacted. The animal's

handling behaviour (e.g. removes fruit pulp but drops seed thereafter, preys on the seed or carries seed away) was also noted.

To investigate the fate of fallen seeds, we carried out removal experiments with marked seeds from October 2010 to January 2011. We selected 10 adult palms at least 100 m away from each other and at least 10 m away from any other conspecific fruiting palm. We used ripe, naturally fallen fruits in paired removal stations. We removed fruit pulp and made a small hole at the tip of each seed. A 50 cm nylon thread (0.45 mm width) was attached to the seed and a flagging tape was fixed at the other end to facilitate the tracking of seeds (Forget and Milleron 1991). Each seed received a unique code in the flagging tape. We placed ten seeds in a removal station beneath the crown of the 10 adult palms and in another removal station set five metres away in a random direction (total of 200 experimental seeds). We checked the seed stations once a week for four months, carefully searching for all tagged seeds within a 20-m radius around the seed stations, a sufficient distance to recover most seeds first cached by rodents (Forget 1990; Kuprewicz 2013). We recorded the number of seeds, the distance the seeds were retrieved and classified them as intact (not moved away); manipulated by animals (i.e. with tooth scars or seed retrieved but not attached to the thread); preyed on; dispersed away (carried > 30 cm away from the seed station with seed intact above the litter or buried); or not found. Between January and March 2011, we ran another removal experiment, but only with ripe fruits (i.e. mesocarp present). Ten fruits were disposed in a station below each fruiting palm (n = 10) used in the seed removal experiments, following the same procedures. These results should be interpreted with caution, since experiments of seed removal were carried out close to the peak of fruit production, while fruit removal experiments were carried out later on when less fruits were available. The availability of fruits/seeds is known to influence the likelihood of hoarding behaviour (Jansen et al. 2004; Haugaasen et al. 2010; Ribeiro and Vieira 2014).

We compared the influence of the presence of fruit pulp in the frequency of different categories of fate with G-tests (Zar 1999). As our data did not follow the assumptions of parametric tests, we ran a factorial analysis of variance with permutations (Anderson and ter Braak 2003). Distance (near or far from the palm) and fate of fruits/seeds (dispersed, intact or not found) were considered fixed treatments. The dependent variable was the number of fruits/seeds in each category of fate. We did not include the categories "preyed on" or "manipulated" in the analysis of variance, because we recorded few events in the former and could not accurately assign a category of fate to most records of the latter (see Results). To evaluate the effect of distance from adult palms on seed fate, an initial analysis was done including data only on cleaned seeds. To investigate the effect of the presence of fruit pulp on seed fate near adult palms, we also compared the removal of cleaned seeds with that of fruits. Statistical analyses were run in R (http://www.r-project.org).

To evaluate the fate of non-dispersed seeds, we collected all seeds found within a 2 × 2 m quadrat established below the crown of 10 non-reproductively active adult palms by the end of November 2011. The seeds were carefully inspected and as-

signed to one out of four categories: intact, preyed on by rodents, preyed on by beetles or rotten. The fate of non-dispersed seeds was compared through an Analysis of Variance (ANOVA) using each palm as a block, random effect factor, considering seed fate categories as fixed treatments and the proportion of seeds in each category at a given palm as the response variable.

To evaluate the importance of seed dispersal for plant regeneration, we mapped all individuals of *A. dubia* found in 10 × 50 m quadrats (n = 10) within a 0.5 ha plot. Palms were assigned to a life-stage category following Pimentel and Tabarelli (2004): seedlings (one or two leaves), juveniles (at least three leaves) or adults (reproductive bunches or evidence of previous reproduction). Each palm was marked and the distance to the nearest adult plant (even if outside the plot) was measured. Seedling and juvenile survival was followed for six months. To describe the spatial distribution pattern of *Attalea dubia* in the 0.5 ha plot, we used the Morisita Index of Dispersion (Id) given by

$$(Id = N.\frac{\sum x^2 - \sum x}{\left(\sum x\right)^2 - \sum x}),$$

where N = number of sample quadrats; Σx = sum of sample counts; Σx^2 = sum of squares of sample counts. The distribution is assumed to be random if $Id = 0$, regular if $Id < 1$ or clumped if $Id > 1$ (Krebs 1998). To evaluate if the spatial distribution deviate from a random pattern, we applied a chi-squared test. To compare the median distance of seedlings and juveniles to the nearest adult palm, we applied a Mann-Whitney U-test. To investigate if seed dispersal by small rodents may account for the spatial distribution of seedlings and juveniles, we classified the mesurements of seed dispersal into classes of 4-m intervals. Then we compared the distribution of the dispersal distances with distances of seedlings and juveniles of adult plants by Kolmogorov-Smirnov tests (Zar 1999).

Results

During visual observations, we obtained 50 records of animals that could potentially disperse the seeds of *Attalea* (see Andreazzi et al. 2009), including *Alouatta clamitans* (brown howler monkey) (62% of records), *Sapajus nigritus* (black-horned tufted capuchin) (20%), *Guerlinguetus brasiliensis* (squirrel) (12%), *Nasua nasua* (coati) (2%) and *Tapirus terrestris* (tapir) (2%). We also obtained 27 photos of mammals with the camera-trap including *G. brasiliensis* (squirrel) (37%), *Philander frenatus* (south-eastern four-eyed opossum) (22%), non-identified nocturnal sigmodontineous rodents (22%), *Didelphis aurita* (big-eared opossum) (4%), *Euryoryzomys russatus* (russet rice rat) (4%) and *Metachirus nudicaudatus* (guianan brown four-eyed opossum) (4%).

During visual observations, 10 visits of groups of *Sapajus nigritus* (Goldfuss, 1809) were observed to fruiting *Attalea*. Each group interacted with a mean of 47

fruits/visit (total of 381 fruits for all visits). They removed the fruits directly from the bunch and ate the mesocarp, spitting and dropping the seeds beneath the palm crown afterwards and providing no dispersal. The squirrel *Guerlinguetus brasiliensis* (Gmelin, 1788) was recorded in six visits and had contact with one seed per visit. Ten other independent records (in different palms) of squirrels were also obtained from the camera-trap data. Squirrels obtained the fruits either from the plant crown or on the ground and moved to another tree. Then they removed the mesocarp, bit into the endocarp and fed on the endosperm. We did not see squirrels hoarding seeds during visual observations, but hoarding behaviour was documented for other *Attalea* species (Carvajal and Adler 2008). The south-eastern four-eyed opossum *Philander frenatus* (Olfers, 1818) was recorded six times at night by cameras-traps, with clear evidence of interaction with fruits in one picture. We obtained six records of non-identified Sigmodontinae rodents (potentially one species of *Oligoryzomys* or *Euryoryzomys*) at night with camera traps and, in one picture, an individual was undoubtedly interacting with a seed. The staff of CBSP stated that woolly-spider monkeys *Brachyteles arachnoides* (Geoffroy, 1806) also feed on fruits of *Attalea*, with similar behaviour to the black-horned tufted capuchin. No birds were recorded interacting with fruits/seeds during visual observations or by camera traps. Therefore, in this study, when we refer to small mammals that potentially disperse seeds of *A. dubia*, we are considering the squirrel *Guerlinguetus brasiliensis*, the marsupial *Philander frenatus* and non-identified nocturnal sigmodontineous rodents.

In total, 46 (15.3%) of fruits and seeds placed on experimental stations were dispersed at a median distance of 3.8 m (range 0.9–15.6 m). Amongst the dispersed fruits/seeds, 39 (85%) were found buried (scatter-hoarded) in soil or under litter, six (13%) above the litter and one (2%) cached amongst the leaves of an epiphytic bromeliad 1 m above ground. Other 47 fruits/seeds (15.6%) were manipulated by animals, including one cleaned seed buried under the seed station, but most of these records (92%) were based on the recovering of broken threads at variable distances from the seed station, without reliable evidence of seed fate. We were not able to find the other 28 fruits and 19 seeds (15.7%) used in the experiments. These fruits/seeds may have been removed further than 20 m from the seed stations and an unknown fraction may have been dispersed or recached. Intact fruits/seeds comprised of 157 records (52.3%) and only two fruits and one seed (total of 1.0%) were found preyed on.

There were differences in the frequency of interactions recorded for fruits and seeds in the removal experiments (G-test, $G = 21.5$, $df = 3$, $P < 0.001$; data from seeds preyed on excluded). The difference was due to a higher frequency of fruits (28.0%) compared to seeds (9.5%) in the category not found. When this category was removed in a subsequent analysis, there was no difference in the frequency of interactions with seeds or fruits ($G = 4.72$, $df = 2$, $P = 0.095$). In the experiment of cleaned seed removal, the distance from an adult palm had no effect on the fate of the seeds (Table 1, Figure 1). There was no interaction between the distance from the adult palm and fate categories (Table 1). Fruits below adult palms had the same chance to interact with animals as cleaned seeds at the same place (Table 1). Most

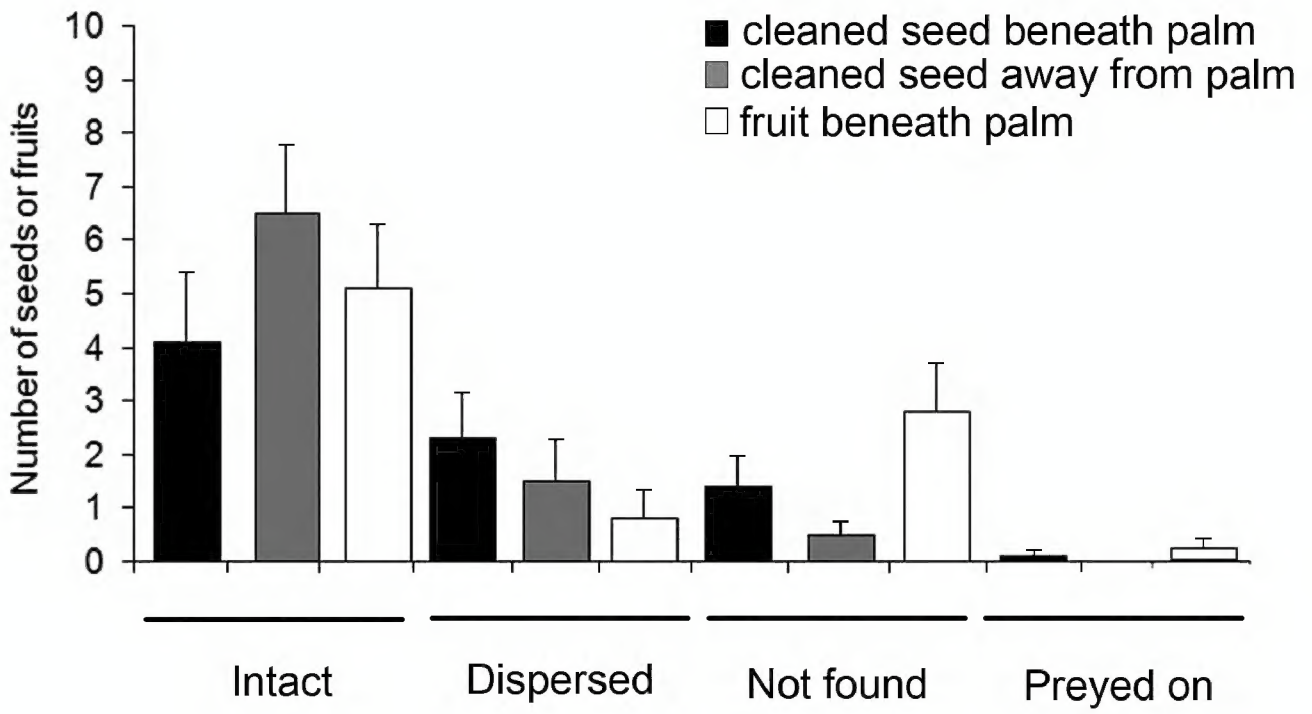


Figure 1. Fate of seeds (n = 200) and fruits (n = 100) of *Attalea dubia* in removal experiments in the floor of an Atlantic Forest in southeast Brazil. Groups of ten cleaned seeds (endocarps) were placed in a station beneath the crown (black bars) or away (grey bars) from fruiting palms (n = 10). Groups of ten fruits (endocarp plus mesocarp) were placed in a station under the crown of the same palms (white bars). Data are mean ± SE.

Table 1. Results from a factorial analysis of variance on 999 permutations of raw data on seed (analysis 1) or seed/fruit (analysis 2) removal experiments. Distance from adult plant (near or far), categories of fate (dispersed, intact or not found) and fruit pulp (presence or not) were entered as fixed factors. See text and Figure 1 for further details.

Effect	d.f.	MS	*F*	P-value
Analysis 1				
Distance from adult palm	1	0.817	0.10	0.753
Category of fate	2	104.62	12.42	0.001
Distance from adult palm x Category of fate	2	17.60	2.09	0.143
Analysis 2				
Fruit pulp	1	21.35	0.16	0.654
Category of fate	2	52.85	6.16	0.004
Fruit pulp x Category of fate	2	12.35	1.44	0.231

fruits/seeds remained intact below palms and there was no interaction between the presence of fruit pulp and seed fate categories (Table 1, Figure 1).

The fate of non-dispersed seeds beneath adult palms was highly variable and not significantly different amongst categories (ANOVA with palms as blocks; categories of seed fate: F = 2.531, df = 3, $P = 0.078$, Figure 2). Many non-dispersed seeds were intact (median of 25.4%; range 8%–90.5%), preyed on by vertebrates (16.7%; 0.0%–66.7%) or rotten (15.5%; 0.0%–88.0%) compared to a median of 0.0% (range 0.0%–16.7%) preyed on by beetles (Figure 2).

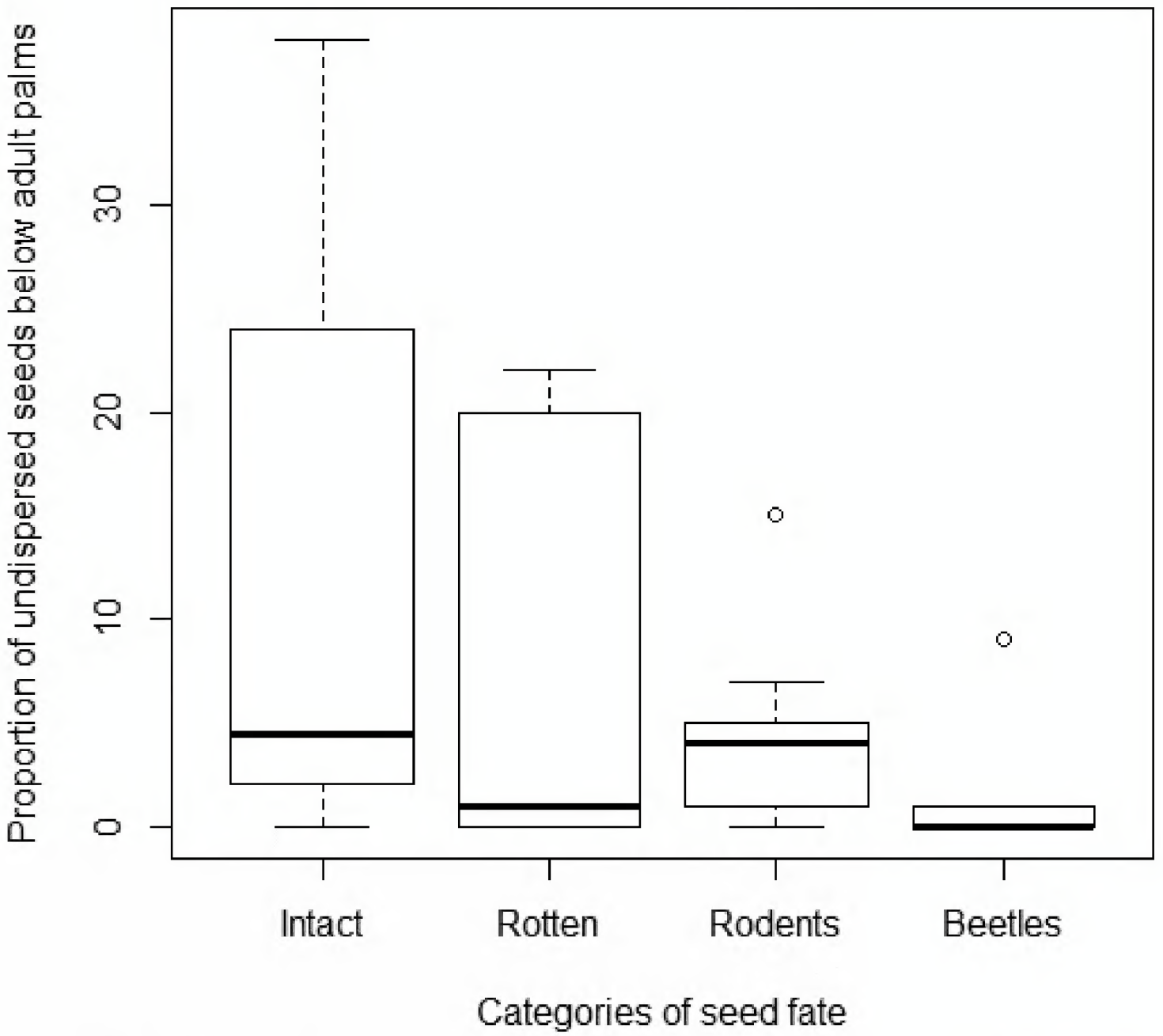
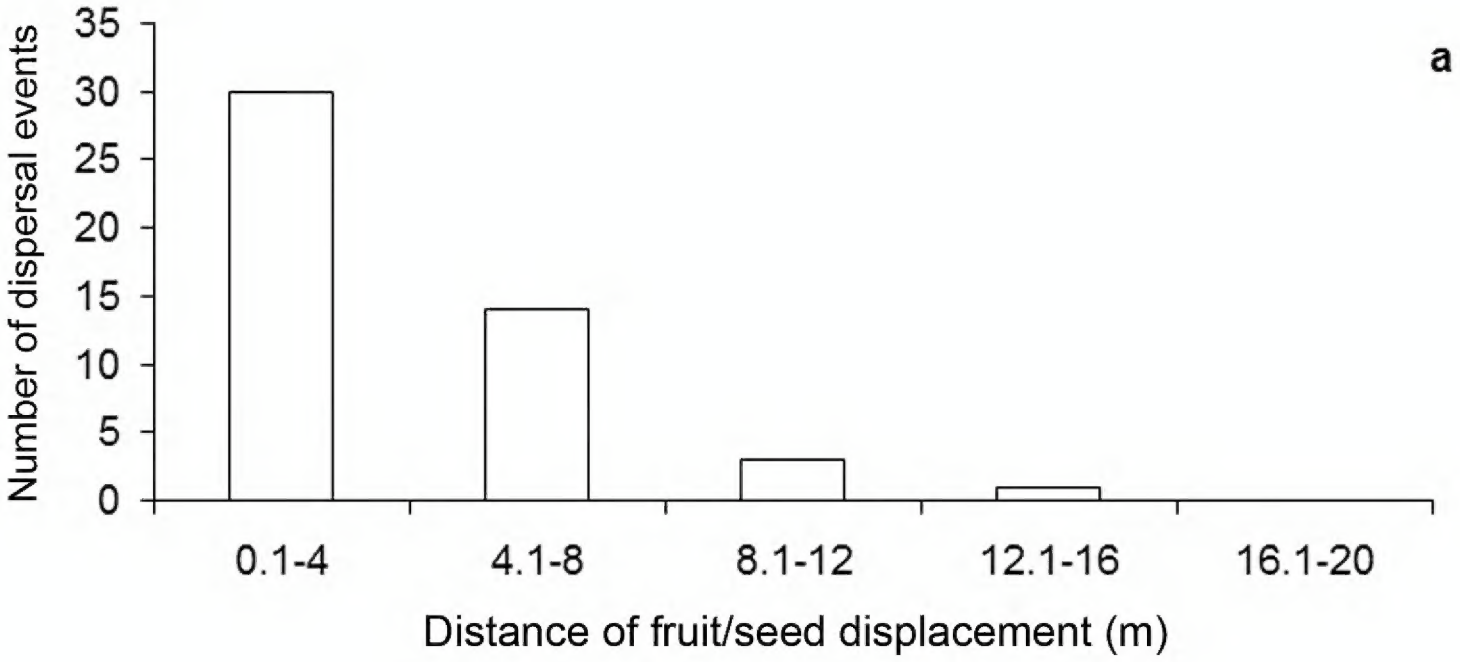


Figure 2. Fate of undispersed seeds (endocarps; n = 253) found in a 2 × 2 m quadrat set below ten adult palms of *Attalea dubia* in an Atlantic Forest in southeast Brazil. Seeds were inspected and included in each of four categories of seed fate: intact, rotten, preyed on by rodents or by beetles. Boxes indicated median and quartile values followed by range.

We found 18 seedlings and 88 juveniles of *A. dubia* in the 0.5 ha plot at CBSP. Seedlings were closer to adult palms (median 8.9 m; range 1.5–20 m) than juveniles (median 14.3 m; range 1.7–26.8 m) (Mann-Whitney U-test, U = 439.5, $P < 0.01$) (Figure 3). A group formed from a merge of data on seedlings plus juveniles showed a clumped distribution pattern within the plot (Morisita Index, Id = 1.5, df = 9, $X^2 = 61.5$, $P < 0.001$). Adult palms were randomly distributed (Id = 0, df = 9, $X^2 = 1$, $P > 0.05$), with a median distance of 18.4 m (range 14.2–38.2 m) from each other. The distribution of fruit/seed dispersal distances provided by small rodents differed from seedling (Kolmogorov-Smirnov test, Maximum deviation = 0.51, $P < 0.01$) and juvenile (Maximum deviation = 0.73, $P < 0.01$) distribution at the same scales (Fig. 3a, b).



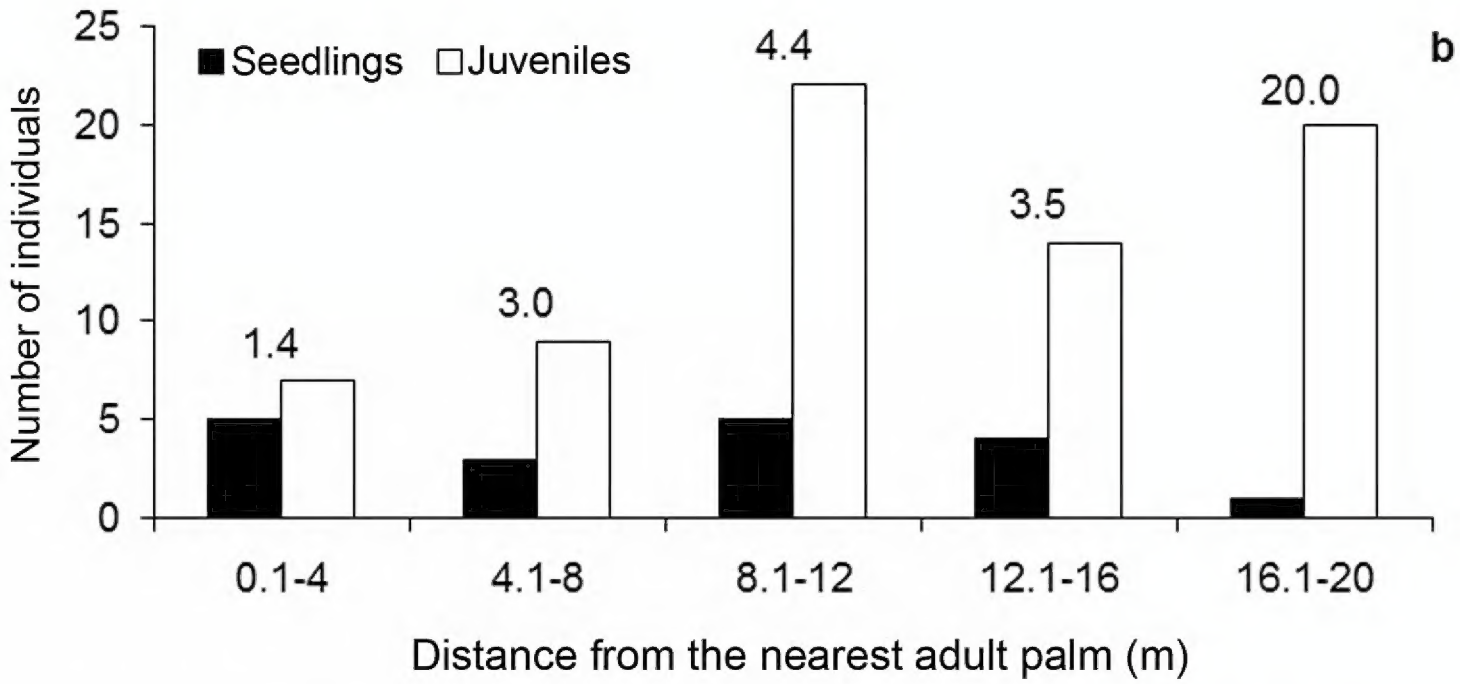


Figure 3. Distances of *Attalea dubia* fruit/seed dispersal by rodents in an Atlantic Forest in southeast Brazil (n = 46 records of recovered fruits/seeds) (**a**). Number of seedlings (n = 18; black bars) and juveniles (n = 88; white bars) in relation to the distance to the nearest adult palm (**b**). The numbers above bars are juvenile/seedling ratios at a given distance class. For both graphs, distances are truncated to 20 m to enable visual comparisons (see text for details).

Discussion

Small mammals provide legitimate dispersal for the large seeds of *Attalea dubia* and probably may allow some plant regeneration in the absence of large mammals in defaunated sites. However, the short distances of seed removal recorded are unlikely to reproduce the spatial distribution of seedlings and juveniles in relation to adult plants observed in the field. This suggests that small mammals, such as squirrels (*Guerlinguetus brasiliensis*), nocturnal Sigmodontinae rodents and marsupials (*Philander frenatus*), can sustain some plant regeneration at local scales, but cannot

account alone for the spatial pattern of *A. dubia* regeneration observed in CBSP and that it would be necessary for the occasional seed dispersal at greater distances from the parental plant by larger mammals to keep the current palm spatial distribution.

Large mammals such as tapirs are known to remove great numbers of seeds, have a large home-range and long gut passage times allowing seeds to be dispersed further away (Fragoso et al. 2003; O'Farrill et al. 2013). We have no records of tapirs consuming the fruits of *A. dubia* during our direct observations. Nevertheless, even if seed dispersal by monkeys (carrying the seed and spitting it far away) and tapirs is rare, the enhanced likelihood of survival away from the parental plants suggests they may contribute disproportionaly to palm recruitment. Tapirs often have a unique role as dispersers of many large seeds (including several *Attalea*) that even large-bodied primates cannot disperse (O'Farrill et al. 2013). Large-bodied frugivores move seeds further and consequently may connect populations through dispersal (Jordano et al. 2007; Giombini et al. 2016; Pérez-Méndez et al. 2016). In our system, the small mammals provide a less efficient dispersal than large mammals considering the possible distances of dispersal and places of deposition. The loss of large animals would truncate distances of seed dispersal to near the parental plants and increase clumpiness and population genetic structure (Jordano et al. 2007; Christianini and Oliveira 2010; Choo et al. 2012; Caughlin et al. 2015; Martins et al. 2016; Pérez-Méndez et al. 2016). However, small mammals may still benefit the regeneration of *A. dubia* even performing dispersal at small spatial scales.

The spatial distribution of seedlings and juveniles at the CBSP suggests that the likelihood of seedling regeneration and the transition from seedling to juvenile stage increases with distance from the parent plant. Regenerants of *A. dubia* showed an aggregated spatial distribution, while adults were randomly distributed suggesting density-dependent mortality in time that decrease the clumpiness at latter stages (Harms et al. 2000; Caughlin et al. 2015). Therefore, seed dispersal by rodents, even at short distances, may increase the chances of palm recruitment, as indicated by the increases in juvenile to seedling ratios at increasing distances from parental plants (Figure 3b). The higher attraction of natural enemies to the surroudings of the parent plant is likely to be the main reason for lower survival in those places, with pathogens, rodents and beetles killing many seeds near the parent palms in CBSP and elsewhere (Meiga and Christianini 2015). Increased seed mortality near the parental palm is also common in other well-protected tropical forests (Wright and Duber 2001; Galetti et al. 2006; Dirzo et al. 2014). Trampling by large mammals attracted to fallen fruits/seeds and leaf fall may also be sources of seedling mortality in the surroudings of the parental palms. Fruiting *Attalea* frequently drop old leaves (3–5 m long, ca. 1.3 m wide), which may produce physical damage to the seedlings and also increase light interception needed for photosynthesis (Vandermeer 1977; Pimentel and Tabarelli 2004). A potential advantage for *A. dubia* to escape seed predators is that its large seed size decreases the risk of embryo damage by small rodents (< 1 kg) as most local species are unable to gnaw the thick and hard endocarp (Galetti et al. 2015). The presence of fruit pulp seems to increase the chance of

removal, as fruits have a higher chance of not being found by us than seeds. Thus, fruit pulp and large seed size combined decrease the potential risks and increase the benefits to the palm seed interacting with rodents.

Removal of seeds away from parent plants by small mammals may increase seed and seedling survival in defaunated sites (see also Cao et al. 2011). Small rodents (< 1 kg) may also cache seeds in low numbers, reducing the risk of density-dependent effects in large clumps of seeds and seedlings, such as near the parent palm or in tapir latrines (Fragoso 1997; Brewer and Rejmánek 1999; Caughlin et al. 2015). Therefore, although small mammals have a lower efficiency in seed dispersal than large animals, they still provide legitimate dispersal. It has been argued that repeated recaching of hoarded seeds by rodents may gradually redistribute seeds at much further distances and even allow regeneration at spatial scales resembling seed dispersal by much larger mammals (Jansen et al. 2012). However, in our study site, we recorded only one recaching of hoarded seeds, which increased the distance of dispersal by just 1.69 m compared to the initial hoarding site. Recaching rate of seeds in CBSP (around 2%) is much lower than that observed in Barro Colorado Island, where 35% of seeds of the palm *Astrocaryum standleyanum* are cached/re-cached to distances greater than 100 m (Jansen et al. 2012). Low seed hoarding and recaching rates by rodents were also observed in the well-protected La Selva Biological Station in Costa Rica (Kuprewicz 2013). Low hoarding and recaching frequencies may be attributed to reduced seasonality in the humid forests of La Selva and CBSP (Beisiegel and Mantovani 2006) compared to seasonally dry forests of BCI (Wright et al. 1999) and the resultant higher levels of year-round variation in food availability. Climate seasonality and its influence in plant phenology and fruit/seed availability for mammals influence caching decisions (Haugaasen et al. 2010; Ribeiro and Vieira 2014). A low seasonality and more regular high resource availability, typical of humid forests such as CBSP (Beisiegel and Mantovani 2006), decrease the likelihood of hoarding behaviour (Jansen et al. 2004, 2012; Haugaasen et al. 2010; Kuprewicz 2013; Ribeiro and Vieira 2014). The low recaching rates could also be due to a lower abundance of agoutis in CBSP compared to other sites. The density of agoutis in CBSP (0.30 individuals/km^2) is the lowest amongst seven large Atlantic Forest remnants where the species is still in present (Galetti et al. 2017) and much lower than that reported for BCI (ca. 20-145 individuals/km^2, Wright et al. 1999). Given the relative scarcity of agoutis at our site, we believe that squirrels and other small rodents play an important role in the fate of seeds. Although, in the Neotropics, some studies mention squirrels only as seed predators (Galetti et al. 1999; Silvius and Fragoso 2002), others suggest that squirrels and other small rodents act as dispersal agents for several plant species in defaunated sites (Brewer and Rejmánek 1999; Bordignon and Monteiro-Filho 2000; Silva and Tabarelli 2001; Pimentel and Tabarelli 2004).

We could not assign the fate of 30% of the fruits/seeds in our removal experiments (sum of categories not found and only broken threads recovered). Those fruits/seeds might have been preyed on or removed further away from the 20 m distance radius where we searched for seeds or even been recached by rodents and

moved to longer distances. The frequency of seed hoarding behaviour seems to be tied to resource availability, with periods of resource abundance favouring hoarding behaviour (Jansen et al. 2004, 2012; Haugaasen et al. 2010; Kuprewicz 2013; Ribeiro and Vieira 2014). Unfortunately, our observations covered only one reproductive year and we cannot evaluate temporal variations in the frequency of hoarding behaviour and its subsequent impact on seed fate and seedling emergence. Therefore, our results should be interpreted with caution and more long term studies would shed light on the temporal variability in hoarding behaviour in the Atlantic Forest, their conditionants and the consequences for plant regeneration (but see Ribeiro and Vieira 2014).

In conclusion, small mammals that often persist in fragmented landscapes (such as squirrels and other small rodents) may perform legitimate seed dispersal that may keep some plant regeneration in the absence of large mammals. Nevertheless, small mammals are unlikely to compensate entirely for the loss of seed dispersal services provided by large mammals (see also Terborgh et al. 2008). Costs of the interaction with small mammals in defaunated sites include some level of seed predation, an increase in clumpiness of early stages of plant regeneration and genetic structure, which have unknown consequences for the long-term survival of LSP in the remnants (but see Caughlin et al. 2015; Martins et al. 2016). Consequently, it is important to highlight that large mammals are irreplaceable and their conservation should be a priority, because they are the only ones able to provide long distances of seed dispersal for LSP and colonise/recolonise distant sites, amongst others, a service of paramount importance for the conservation of tropical forest biodiversity.

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